

## **Dragons fly, biologists classify: an overview of molecular odonate studies, and our evolutionary understanding of dragonfly and damselfly (Insecta: Odonata) behavior**

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Among insects, perhaps the most appreciated are those that are esthetically pleasing: few capture the interest of the public as much as vibrantly colored dragonflies and damselflies (Insecta: Odonata). These remarkable insects are also extensively studied. Here, we review the history of odonate systematics, with an emphasis on discrepancies among studies. Over the past century, relationships among Odonata have been reinterpreted many times, using a variety of data from wing vein morphology to DNA. Despite years of study, there has been little consensus about odonate taxonomy. In this review, we compare odonate molecular phylogenetic studies with respect to gene and model selection, optimality criterion, and dataset completeness. These differences are discussed in relation to the evolution of dragonfly behavior.

**Keywords:** Odonata; mitochondrion; nuclear; phylogeny; systematic; dragonfly; damselfly

### **Introduction**

#### ***Why study Odonata?***

The order Odonata comprises three suborders: Anisozygoptera, Anisoptera, and Zygoptera. There are approximately 6000 species of Odonata described worldwide (Ardila-Garcia & Gregory, 2009). Of the three suborders Anisoptera and Zygoptera are by far the most commonly observed and collected, because there are only two known species of Anisozygoptera under the genus *Epiophlebia*. All odonate nymphs are aquatic, with a few rare exceptions such as the semi-aquatic *Pseudocordulia* (Watson, 1983), and adults are usually found near freshwater ponds, marshes, rivers (von Ellenrieder, 2010), streams, and lakes (although some species occur in areas of mild salinity; Corbet, 1999).

Dragonflies and damselflies are a recurring feature in folklore (Sarot, 1958), with some cultures representing them as a sinister omen and others using them as symbols of good luck, speed and clean water. Odonata have medicinal uses in Eastern culture and have been the subjects of

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visual art, jewelry, and pottery for centuries (Sarot, 1958). Ecologically, Odonata are considered by many to be important because the presence of some species may indicate ecosystem quality (Catling, 2005). Odonate biodiversity is affected by the flow and turbidity of water as well as the presence and type of vegetation (Corbet, 1999). The co-occurrence of other animals can influence ovipositing female choice of odonate nymphal habitats and resulting nymphal survivorship, because the bulk of the nymphal diet comprises animals from lower trophic levels while higher trophic level predators, such as fish, impose strong predation pressure on nymphs (e.g. Corbet, 1999; Hovmöller & Johannson, 2002; Wittwer, Sahlén & Suhling, 2010). Despite public misconceptions, dragonflies and damselflies are considered by many to be beneficial as they eat human pests such as mosquitoes, flies and gnats.

Over the last 150 years (e.g. Martin, 1907; Ris, 1909–1919; Tillyard, 1917), the three suborders of Odonata have been well studied, yet their systematic relationships remain in debate. Here we give an overview of the current state of each suborder's taxonomy. The suborder Anisozygoptera comprises mainly fossil species, and in its broad sense is probably not monophyletic. Only one extant family (Epiophlebiidae) is generally placed here (although it has been considered by some to be a family in Anisoptera; Schorr, Lindeboom & Paulson, 2010), with one genus (*Epiophlebia*) containing two species, *E. superstes* (Selys, 1889) found in Japan and *E. laidlawi* (Tillyard, 1921), found in Nepal. The morphology of epiophlebiids is considered by many to be intermediate between Anisoptera and Zygoptera with moderate sized, thick yellow- and black-banded bodies and petiolate wings. The more speciose suborder Anisoptera, with over 300 genera and 2924 species, is currently considered to comprise 11 families: Aeshnidae, Austropetaliidae, Chlorogomphidae, Cordulegastridae, Corduliidae, Gomphidae, Libellulidae, Macromiidae, Neopetaliidae, Petaluridae, and Synthemistidae (Schorr et al., 2010), although this taxonomy will likely need to be revisited in light of recent molecular results (e.g. Bybee, Ogden, Branham & Whiting, 2008; Carle, Kjer & May, 2008; Dumont, Vierstraete & Vanfleteren, 2010). Adult dragonfly eyes are separated by less than one dorsal diameter and the wing pairs are dissimilar, with the hind wings broader at the base than the forewings (*aniso* = unequal). Nymphs have internal gills, or rectal pads, and relatively stout bodies. The third suborder, Zygoptera, comprises 20 putative families: Amphipterygidae, Calopterygidae, Chlorocyphidae, Coenagrionidae, Dictteriidae, Euphaeidae, Hemiphlebiidae, Isosotictidae, Lestidae, Lestoideidae, Macromiidae, Megapodragonidae, Perilestidae, Philogangidae, Platycnemididae, Platystictidae, Polythoridae, Protoneuridae, Pseudolestidae, and Synlestidae with 200 genera and 2901 species (Schorr et al., 2010). Zygoptera are generally slender bodied and delicate in appearance and their eyes are more widely separated than in dragonflies. Damselfly forewings and hind wings are alike in shape (*zygo* = joined) with either dense or sparse venation. Across the two principle suborders, family-level taxonomy is in debate, although less so in the Anisoptera, and further revisionary work is sorely needed.

## Review and prospects

### *Causes of confusion in past odonate work*

Traditionally, odonate systematic study has relied heavily on morphological data, which is the cornerstone of taxonomic work. Many morphological studies of Odonata, however, have focused on wing vein characters (e.g. Bybee et al., 2008; Carle & Kjer, 2002; Polhemus, 1997; Rehn, 2003; Trueman, 1997) that may be homoplasious. Despite progress in understanding homologies in Odonata venation, many characters may support convergent relationships when used to the exclusion of other characters (see Carle et al., 2008 for further discussion of this topic). For example, Carle et al. (2008) suggest that reduced wing venation has resulted in the erroneous grouping

of protoneurines and disparoneurines (Zygoptera) in most taxonomies. Many Zygoptera share dense wing venation patterns, as in the Calopterygoidea, while others have sparse venation like Coenagrionidae and Lestidae. Comparing taxa thus becomes challenging. To further complicate matters, flight style may have led to convergence in wing venation, as anisopteran gliders, for example, tend to have expanded anal vein regions, possibly to reduce energy expenditure (Corbet, 1999). In general, wing-vein based odonate systematic study has provided conflicting views about the basalmost nodes within Odonata and the position of Anisozygoptera with respect to Anisoptera.

### ***Molecular systematics of Odonata***

Molecular research was first thought by many to be a method to reduce subjectivity and lessen taxonomic confusion. For Odonata, this has not always proven to be the case, with molecular phylogenies of Odonata often disagreeing with both morphological results and each other. Several early molecular studies attempted to resolve subordinal relationships (e.g. Misof, Rickert, Buckley, Fleck & Sauer, 2001; Saux, Simon & Spicer, 2003; see Table 1). Others focused on resolving debates about generic and intergeneric relationships, e.g. Chippindale, Davé, Whitmore & Robinson (1999; *Ischnura*), Kambhampati & Charlton (1999; *Ladona*, *Plathemis*, *Libellula*), Brown, McPeck & May (2000; *Enallagma*), Misof, Anderson & Hadrys (2000; *Calopteryx*), Artiss, Schultz, Polhemus & Simon (2001; *Ladona*, *Plathemis*, *Libellula*), Hovmöller & Johansson (2002; *Leucorrhinia*), Jordan, Simon & Polhemus (2003; *Megalagrion*), and Caesar & Wenzel (2009, *Argia*). Odonata were included in larger studies of Insecta (e.g. Kjer, 2004; Kjer, Carle, Litman & Ware, 2006), and of the Paleoptera (Ogden & Whiting, 2003). Major family-level molecular studies aimed to resolve intergeneric relationships and reconstruct subfamily relationships. For some taxa, such as in Libellulidae (e.g. Pilgrim & von Dohlen, 2008; Ware, May & Kjer, 2007) various gene combinations (with and without morphology) yielded similar low resolution results. This is likely due to the fact that there are short internodes separating putative subfamilies, indicating that there was a rapid radiation in Libellulidae in a relatively short period of geologic time.

### ***Taxonomy and molecular results***

Not all molecular studies have disagreed with previous morphology based taxonomy. Anisopteran families Aeshnidae, Gomphidae, Petaluridae, Cordulegastridae, Macromiidae, and Libellulidae are supported by molecular work (e.g. Bybee et al., 2008; Carle et al., 2008; Kjer et al., 2006; Ware et al., 2007). Corduliidae *sensu lato* has been found by several authors to be paraphyletic (e.g. Bybee et al., 2008; Ware et al., 2007). There have been several examples of molecular studies that revealed phylogenetic relationships not previously considered by morphology (e.g. *Celithemis*, *Leucorrhinia*, and *Sympetrum*; Pilgrim & von Dohlen, 2008). In Zygoptera, most molecular data do not support the monophyly of Platynemididae, Protoneuridae (e.g. Carle et al., 2008), Synlestidae, Coenagrionidae, Megapodagrionidae, Amphipterygidae (Bybee et al., 2008) and Calopterygoidea (Carle et al., 2008; Dumont et al., 2005). Most studies have been cautious about renaming taxonomic groups based on molecular studies; e.g. Ware et al. (2007) found that non-corduliine “Corduliidae” form a well-differentiated clade distinct from Corduliidae *sensu stricto*, but these authors gave the former an informal name, the GSI (Gomphomacromiinae, Synthemistinae, and Idionychinae), pending further work. On the other hand, Ware et al. (2007) suggest that Macromiinae (Anisoptera) be elevated to family level status (Macromiidae), supporting Gloyd’s (1959) morphological study, and Carle et al. (2008) reduced the rank of the zygopteran family Pseudostigmatidae to subfamily rank within Coenagrionidae.

Table 1. A comprehensive list of molecular odonate studies, the genes implemented in the study, and the size of the molecular dataset. \* = aligned with reference to secondary structure; \*\* = whole mitochondrial genome was treated as having each fragment for calculations.

Study	Mitochondrial genes								Nuclear genes							Total number of basepairs	*
	COI	COII	Cytb	tRNA	ND1	12S	16S	Genome**	ITS1	ITS2	5.8S	18S	28S	H3	EF1A		
Chippindale et al., 1999: Odonata: Zygoptera: Coenagrionidae: <i>Ischnura</i>	X	Yes	X	X	X	Yes	X	X	X	X	X	X	X	X	X	1205	No
Kambhampati and Charlton, 1999: Odonata: Anisoptera: Libellulidae: <i>Plathemis</i> , <i>Ladona</i> , <i>Libellula</i>	X	X	X	X	X	X	Yes	X	X	X	X	X	X	X	X	419	Yes
Brown et al., 2000: Odonata: Zygoptera: <i>Enallagma</i>	Yes	Yes	X	Yes	X	X	X	X	X	X	X	X	X	X	X	842	N/A
Misof et al., 2000: Odonata: Zygoptera: Calopterygidae: <i>Calopteryx</i>	X	X	X	X	X	X	Yes	X	X	X	X	X	X	X	X	546	No
Misof et al., 2001: Odonata	X	X	X	Yes	X	Yes	Yes	X	X	X	X	X	X	X	X	1540	Yes
Artiss et al., 2001: Odonata: Anisoptera: Libellulidae: <i>Plathemis</i> , <i>Ladona</i> , <i>Libellula</i>	Yes	X	X	X	X	X	Yes	X	X	X	X	X	X	X	X	1151	No
Weekers et al., 2001: Odonata: Zygoptera: Calopterygidae: <i>Calopteryx</i>	X	X	X	X	X	X	X	X	Yes	Yes	Yes	X	X	X	X	1136	No
Hovmoller & Johansson, 2002: Odonata: Anisoptera: Libellulidae: <i>Leucorrhinia</i>	X	X	X	X	X	X	X	X	Yes	Yes	Yes	X	X	X	X	782	No
Misof & Fleck, 2003: Odonata	X	X	X	X	X	X	Yes	X	X	X	X	X	X	X	X	~600	Yes
Saux et al., 2003: Odonata	X	X	X	X	X	Yes	X	X	X	X	X	X	X	X	X	346	Yes
Ogden & Whiting, 2003: Odonata	X	X	X	X	X	X	X	X	X	X	X	Yes	Yes	Yes	X	Not reported	No
Jordan et al., 2003: Odonata: Zygoptera: Coenagrionidae	X	Yes	X	Yes	X	X	X	X	X	X	X	X	X	X	Yes	2326	N/A

Yamauchi et al., 2004: Odonata: Anisoptera: <i>Orthetrum triangulare melania</i>	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	X	X	X	X	X	X	X	14,033	N/A
Kjer, 2004: Odonata	X	X	X	X	X	X	X	X	X	X	X	Yes	X	X	X	2319	Yes
Dumont et al., 2005: Odonata: Zygoptera: Calopterygidae	X	X	X	X	X	X	X	X	Yes	Yes	Yes	Yes	X	X	X	2745	Yes
Jordan, Simon, Foote & England, 2006: Odonata: Zygoptera: <i>Megalagrion</i>	X	Yes	X	X	X	X	X	X	X	X	X	X	X	X	Yes	1702	N/A
Kjer et al., 2006: Odonata	Yes	Yes	X	Yes	X	Yes	Yes	X	X	X	X	Yes	Yes	Yes	Yes	14,209	Yes
Kiyoshi & Sota, 2006: Odonata: Anisoptera: <i>Davidius</i>	Yes	Yes	X	Yes	X	X	X	X	Yes	Yes	Yes	Yes	X	X	X	1851	No
Hasegawa & Kasuya, 2006: Odonata	X	X	X	X	X	X	Yes	X	X	X	X	Yes	X	X	X	3580	Yes
Groeneveld et al., 2006: Odonata: Zygoptera: Pseudostigmatidae	X	X	X	X	Yes	X	Yes	X	X	X	X	X	X	X	Yes	1240	No
Stoks & McPeck, 2006: Odonata: Zygoptera: <i>Lestes</i>	Yes	Yes	X	Yes	Yes	X	Yes	X	X	X	X	X	X	X	X	2095	Not reported
Dijkstra, Groeneveld, Clausnitzer & Hadrys, 2007: Odonata: Zygoptera: <i>Pseudagrion</i>	X	X	X	Yes	Yes	X	Yes	X	X	X	X	X	X	X	X	610	No
Ware et al., 2007: Odonata: Anisoptera: Libelluloidea	X	X	X	X	X	X	Yes	X	X	X	X	X	Yes	X	X	1418	Yes
Pilgrim & von Dohlen, 2008: Odonata: Anisoptera: Libellulidae	X	X	X	X	X	Yes	Yes	X	X	X	X	X	X	X	Yes	2448	Yes
Bybee et al., 2008: Odonata	X	Yes	X	X	X	Yes	Yes	X	X	X	X	Yes	Yes	Yes	X	2160	No
Ware et al., 2008: Odonata: Anisoptera: Libelluloidea	X	X	X	X	X	X	Yes	X	X	X	X	X	Yes	X	X	1418	Yes
Kiyoshi, 2008: Odonata: Anisoptera: <i>Anotogaster</i>	Yes	Yes	X	X	X	X	X	X	X	X	X	X	X	X	X	845	N/A
Fleck et al., 2008a: Odonata: Anisoptera	X	X	X	Yes	X	Yes	Yes	X	X	X	X	X	X	X	X	2026	Yes

(Continued)

Table 1. Continued.

Study	Mitochondrial genes								Nuclear genes							Total number of basepairs	*
	COI	COII	Cytb	tRNA	ND1	12S	16S	Genome**	ITS1	ITS2	5.8S	18S	28S	H3	EF1A		
Fleck et al., 2008b: Odonata: Anisoptera: Libellulidae: Trithemistinae	X	X	X	Yes	X	Yes	Yes	X	X	X	X	X	X	X	X	2026	Yes
Carle et al., 2008: Odonata	X	X	X	X	X	Yes	Yes	X	X	X	X	Yes	Yes	X	Yes	8483	Yes
Dumont et al., 2010: Odonata	X	X	X	X	X	X	X	X	Yes	Yes	Yes	Yes	X	X	X	Not reported	No
Ware et al., 2009: Odonata: Anisoptera: Libelluloidea: Synthemistidae	Yes	X	X	X	X	X	Yes	X	X	X	X	X	Yes	X	X	3148	Yes
Damm, Dijkstra & Hadrys, 2010a: Odonata: Anisoptera: Libellulidae: <i>Trithemis</i>	Yes	X	X	X	Yes	X	X	X	X	X	X	X	X	X	X	1126	N/A
Damm et al., 2010b: Odonata: Anisoptera: Libellulidae: <i>Trithemis</i>	Yes	X	X	X	Yes	X	X	X	X	X	X	X	X	X	X	1126	N/A
Lin et al., 2010: Odonata: Zygoptera: Polythoridae: <i>Euphaea formosa</i>	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	X	X	X	X	X	X	X	15,912	N/A
Lee et al., 2010: Odonata: Anisoptera: Gomphidae	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	X	X	X	X	X	X	X	14,033	N/A
Caesar & Wenzel, 2009: Odonata: Zygoptera: Coenagrionidae: <i>Argia</i>	X	X	X	X	X	X	Yes	X	X	X	X	X	X	X	X	551	No
Percentage of studies using gene fragment	32.4	29.7	8.1	32.4	21.6	32.4	56.8	8.10	13.5	13.5	13.5	24.3	18.9	8.1	16.2	Average number of basepairs = 3027	Less than 50% aligned ribosomes with reference to secondary structure
Percentage using each gene independently*** of the other, i.e. not combined (***) = percentage using both nuclear and mitochondrial fragments = 28%)					56%										16%		

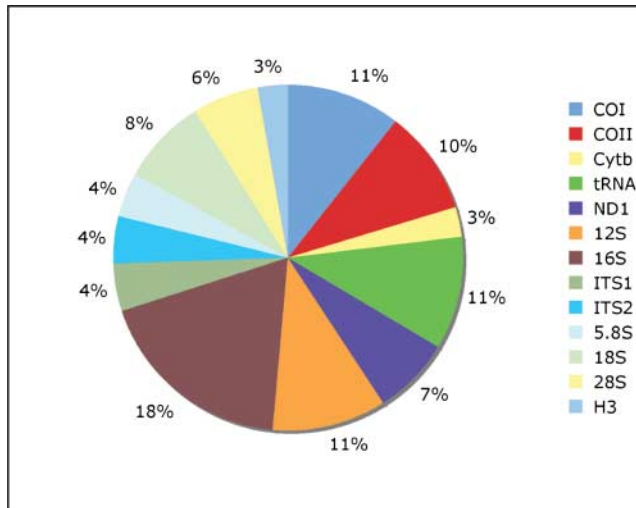


Figure 1. Gene fragments used in molecular studies of Odonata. Numbers indicate percentages; N = 29. Abbreviations: COI, cytochrome oxidase I; COII, cytochrome oxidase II; Cytb, cytochrome B; ND1, NADH 1; 12S, small mitochondrial ribosome; 16S, large mitochondrial ribosome; ITS1, internal transcribed spacer 1; ITS2, internal transcribed spacer 2; 5.8S, a non-coding region of the ribosome; 18S, small nuclear ribosome; 28S, large nuclear ribosome; H3, histone 3; EF1A, elongation factor 1-alpha.

### *Agreement, disagreement, and reasons for discrepancies among studies*

Although Misof et al. (2001) suggested that mitochondrial ribosomal markers may not be capable of recovering the true tree of Anisoptera due to signal decay, they have continued to be a popular gene choice (20% of studies used this marker; Figure 1). In general, there has not been much consensus with regards to gene choice (see Figure 1), although the ITS1 or ITS2 region (i.e. the internal transcribed spacer regions of the ribosome, a section that is notoriously difficult to align), has been more rarely sequenced. Mitochondrial genes have been shown to evolve faster and so are more frequently used to examine relationships at the species level, while nuclear genes are more commonly used when resolving higher level splits. There has also been debate over how to align ribosomal data, which has been shown to affect phylogenetic reconstruction (Kjer, 1995; Kjer, Gillespie & Ober, 2007). Many choose a manual alignment (secondary structure alignment) because it has strong support as the most accurate currently available method of aligning ribosomal data. Several studies have shown this to be so (Gillespie et al., 2005; Kjer, 1995, Kjer et al., 2007; Mugridge et al., 2000). Some, however, have not used manual alignment (Artiss et al., 2001; Bybee et al., 2008; Caesar & Wenzel, 2009; Chippindale et al., 1999; Groenevelde, Clausnitzerb & Hadrys, 2006; Hovmoller & Johansson, 2002; Misof et al., 2000; Ogden & Whiting, 2003; Weekers, De Jonckheere & Dumont, 2001), which might account for part of the variation among studies. Twenty-nine percent of studies incorporated at least two independent gene fragments, although other studies used morphology as a second independent dataset. Further complicating the debate is the fact that phylogenetic reconstructions may differ depending on the optimality criterion used (parsimony, likelihood, Bayesian likelihood).

### *What are the implications of these discrepancies?*

Phylogenetic information serves multiple purposes, from informing taxonomic work, to supporting conservation initiatives, to exploring odonate ecology. When molecular studies disagree, we see different hypotheses supported. Pfau's (2005) study on the vesica spermalis (sperm pump) in

the secondary genitalia of male Anisoptera suggested a phylogenetic arrangement (recently revised in Pfau, 2011) that has been partially supported (Dumont et al., 2010), and disputed (Bybee et al., 2008; Carle et al., 2008; Fleck et al., 2008a). Our understanding of the evolution of nymphal gills, which are used for respiration in the aquatic juvenile stage of odonates, from external caudal lamellae in Zygoptera to internal rectal pads in Anisoptera, may not be fully appreciated until the relationships among zygopteran families are resolved. The evolution of exophytic oviposition, via a reduced or vestigial ovipositor in Libelluloidea and Gomphidae, has been suggested to have been convergently derived (e.g. Carle et al., 2008; Misof et al., 2001, reduced dataset phylogeny). Gomphidae and Libelluloidea are not normally considered sister groups, but a sister-group relationship between Gomphidae and Libelluloidea has been supported by other molecular studies (e.g. one tree of Bybee et al., 2008b; Dumont et al., 2010; Fleck et al., 2008; Misof et al., 2001, unadjusted dataset phylogeny). In Anisoptera, our understanding of the evolution of countless morphological structures, from the basal wing sclerites to the male secondary genitalia, varies depending on the phylogenetic hypothesis an author chooses to use.

### ***Dating analyses***

The first molecular dating analysis of Odonata focused on the damselflies Calopterygoidea (Dumont et al., 2005). Using 18S, 5.8S, ITS1 and ITS2 these authors recovered a dated tree that suggested that Calopterygoids started radiating approximately 160 million years ago. Using similar methodology, Ware, Ho and Kjer (2008) and Ware, Simaika and Samways (2009) recovered dated trees of libelluloid dragonflies, which suggested that the superfamily arose approximately 200 million years ago. Since then, the field of molecular dating has advanced and simplified with the advent of user-friendly interfaces such as BEAST (Drummond & Rambout, 2007). Although the molecular dating of Odonata is still in its infancy, it has already drawn harsh criticism from paleo-odonatologists; Fleck, Waller, Serafin and Nel (2009a) criticized Dumont et al. (2005) for misusing stem group fossils during the calibration step of their molecular dating analysis of extant taxa, and Fleck et al., (2009b) criticized Ware et al. (2008) – in our view mistakenly – for not including all potentially informative fossils (using minimum and maximum calibrations does not require all fossils to be included, but rather just the oldest and youngest ones). Part of the difficulty in defending molecular dating results lies in the fact that they are often substantially older than fossil records might suggest: a quick review of dating and fossil odonate literature reveals that Dumont et al. (2005) recovered ages that are older than fossil records by 100 million years and Ware et al. (2008) dates older than the oldest fossil Libelluloidea (Lissagomphidae) by roughly 40 million years. Branch length error may mislead molecular dates (e.g. Brown et al., 2008; Phillips, McLenachan, Down, Gibb & Penny, 2006), because of gene incongruence (e.g. Springer, Murphy, Eizirik & O'Brien, 2003), model selection (e.g. Ware et al., 2008) or calibration error (e.g. Brochu, 2004). Similarly, discrepancies may occur in comparison of fossil data (relying on post-speciation accumulated morphological changes) and molecular data (relying on sequences that also have accumulated genetic changes pre-speciation), i.e. genotype–phenotype discrepancy (Brown et al., 2008). Furthermore, the disagreement among paleontologists with regard to the assignment of certain fossils to particular families or subfamilies makes it more difficult to eliminate those discrepancies. Nucleotide bias and among site and among taxa rate variation also potentially influence molecular dating results, although this has not yet been thoroughly studied in insects. As more work is done in this field, it is possible that molecular ages of Odonata will become more precise and accurate, increasing our confidence in them while also reducing the divide among paleo- and neo-odonatologists (Ware & Grimaldi, 2011).



### The next decade of odonate molecular work

As new species are described, they will contribute to our increased molecular taxon sample, which might aid in phylogenetic resolution and increased nodal support (e.g. Dow, 2010 – zygopteran *Drepanosticta sbong* and *Protosticta tabau* from Borneo; Pinto & Carvalho, 2010 – anisopteran *Lauiromacromia* from Brazil; Kalkman, Richards & Polhemus, 2010 – zygopteran *Argiolestes* from Papua New Guinea). As threatened species are studied (e.g. Clausnitzer et al., 2010), molecular data may prove useful for identifying populations with unique haplotypes or those isolated from gene flow (e.g. barcoding, Damm, Schierwater & Hadrys, 2010b). Despite great progress in the field of molecular odonatology, morphology remains the cornerstone to which all molecular work should be compared and evaluated. Combined molecular and morphological datasets (e.g. Bybee et al., 2008) may allow extant and extinct taxa to be evaluated in the same phylogenetic framework. Whole genome sequencing is becoming more widely available and affordable, and three odonate taxa now have their entire mitochondrial genome sequenced: *Davidius lunatus* (Anisoptera: Gomphidae; Lee et al., 2010); *Euphaea formosa* (Zygoptera: Polythoridae; Lin, Chen & Huang, 2010); and *Orthetrum triangulaire melania* (Anisoptera: Libellulidae; Yamauchi, Miya & Nishida, 2004). The future of odonate systematics is bright, although there remains the need for novel molecular markers, greater taxon samples for which we have whole genome information, and consideration of how molecular and morphological data interact in the reconstruction of phylogenetic hypotheses.

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